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THE MECHANISM OF ROOT CURVATURE.[1]

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(WITH ONE FIGURE)

Introduction.

THE question as to the mechanism by means of which growing plant organs respond to external stimuli has engaged the attention of writers on the phenomena of plant life during the last hundred and fifty years. Some of the earlier writers supposed that plants turned toward the sunlight because the heat of the sun contracted the plant fibers on the side toward the light (1, 26). Du Hamel (15) assigned light as the cause of movement of leaves. He knew that stems grew upward in the dark and hence were not influenced in the direction of their growth by light alone, as had been supposed previously.

In 1806 Knight (31) published his classical experiments with seeds germinated on rapidly revolving wheels, and he found that the roots grew outward, and the stems inward toward the center of revolution. Knight drew the conclusion that gravitation is the force that causes roots of seedlings to grow down and stems

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[1] The experiments reported in this paper were carried out at the University of Michigan in connection with work for the degree of Doctor of Science, under the direction of Professor V. M. Spalding. I wish to express my hearty thanks to both Professor Spalding and Professor F. C. Newcombe for many helpful suggestions and for the facilities of the botanical laboratory which were placed so unreservedly at my disposal.

to grow upward. This conclusion holds good to the present time, but Knight's explanation of how gravitation could affect roots so differently from stems is of historical interest only. He considered the root curvature as a purely passive bending due to great flexibility in the curving zone.

After Knight we need take no special notice of the explanations given of curvature in growing plant organs until the time of Hofmeister and Frank, though several authors (**4, 16, 40, 70**) wrote upon the subject in the interval. The two men named engaged in a controversy as to whether the curve which takes place in roots that are placed in a horizontal position is purely passive as claimed by Hofmeister (**27, 28**), or is an active curvature as asserted by Frank (**21, 22**). The latter proved his point by showing experimentally that the curving root can be made to lift a weight. Frank also introduced the term *geotropism* to designate the response of plant organs to the action of gravitation.

Sachs, in his earlier work (**61**), explained the curvature of plant organs by supposing a difference in the rate of growth on the opposite sides of the curving organ. Later, influenced by the work of de Vries (**71-75**), he regarded the difference in growth of the two sides as conditioned by greater turgor on the convex side. De Vries's conclusions rested principally on the fact that plant organs in the early stages of curvature are completely straightened on plasmolysis, and he supposed the cells of the convex side must have been more highly stretched by osmotic pressure. The osmotic substances that were especially effective were said to be organic acids and their salts (**75**).

Sachs has added much to our knowledge of curvatures produced in plant organs by external stimuli. In his investigation of roots (**62**) he found that the cortex of roots grows faster than the axial strand, that split roots curve with the cut face concave, and that any part of the cortex derives its nutriment from that part of the axial strand lying in the same transverse zone. He found by external measurement, as well as by microscopical

measurement of cells, that in geotropically curved roots the con-
vex side grows only a little faster than the normal root, while
the strong curve is produced by the much reduced growth of
the under side (**62**, p. 463). In another paper (**63**) he used
stems of several dicotyledonous plants of different families, and,
after separating different tissues of stems curved geotropically,
he found that the concave cortex grows less and the convex
cortex more than the corresponding parts in normal stems.
Also the pith grows faster than cortex, and the relation of pith
to cortex is such that in curved stems the tension is increased
on the concave side and diminished on the convex side.

An interesting paper by Ciesielski (**5**) furnishes some valuable
experiments in connection with root curvature, though his explana-
tion of the curve is of no value. He was the first to assert that
the removal of the root tip prevented the root from curving as
usual when it was placed in a horizontal position. He cut off the
cortex of roots on one side down to the axial strand, and when
this side was turned downward with the root laid in a horizontal
position the curve formed more rapidly and its radius was smaller
than in the normal root under the same conditions. If such a
root is laid with the cut face upward, in the majority of cases it
curves downward likewise, though more slowly. Sometimes it
curves upward at first and only afterward does it curve downward
(**5**, p. 19). The significance of these experiments will be discussed
later.

Kraus (**35**) investigated juice pressed out from the separated
convex and concave halves of curving stems, and found, contrary
to the theory of de Vries, that osmotic substances diminished
both relatively and absolutely on the convex side during the prog-
ress of the curve. Hence the curve cannot be produced by an
increase of such substances on that side.

Charles Darwin (**9**, **10**) gave a new impetus to investigation
of curvatures produced by stimuli. His conclusion that the root
tip performs a function similar to that of the brain in lower
animals (**10**, p. 573) called out a great number of articles both
for and against it, and the controversy only ended in 1894 when

Pfeffer (57) proved that Darwin was right, and that the root tip alone is sensitive to external stimuli, and the stimulus is transmitted to the part of the root in which the curve takes place, a distance which may be as much as ten millimeters. Darwin was also the first to show that injury to one side of the root tip may act as a stimulus, causing the root to curve away from the side injured. He regarded curvatures in growing organs as modifications of circumnutation, and thought the immediate cause was a difference in turgescence of the cells on opposite sides of a curving organ. In the work called out by Darwin's *Power of movement in plants* a number of new theories were evolved as to the mechanism of root curvature, and at first the theories had a very close relation to the question of the function of the root tip. Detlefsen opposed Darwin's view (13), but his purely mechanical explanation of the mechanism of curvature has been shown by Spalding (69, p. 442) to be untenable. Spalding adopts the term *traumatropism*, proposed by Pfeffer (56, p. 374) to designate a response of plant organs to the stimulus of injury or wounding, and this term has now been generally accepted.

Wiesner was probably Darwin's most vigorous opponent, and in several papers of considerable length (76–78) he discusses growth-curvatures in both stems and roots. He presents an explanation of these curvatures which, in a somewhat modified form, has been adopted by some of the most recent writers on the subject. He accounts for the traumatropic curvature of roots, which he calls the Darwinian curve, by an increased ductility of the cell membranes on the injured side. The turgor in these cells then stretches them more rapidly than those of the opposite side, with the result that a curve is produced whose convexity is on the injured side (78, pp. 268–9). The membranes of the convex side are not only more ductile, but also less elastic than those of the concave side. This condition is also favorable to the formation of a curve. The experimental evidence offered by Wiesner in support of his explanation of the curve was the fact that roots injured by decapitation grew faster than normal ones if they were grown in water, and even in those

grown in a moist chamber the partial growth in the zone of the traumatropic curve was greater than in the corresponding zone of normal roots, though the total growth of those in the moist chamber was less in decapitated than in uninjured ones.

In looking for an explanation of growth-curvatures which would apply to both unicellular and multicellular organs, Wortmann thought he had discovered the cause in the aggregation of the protoplasm on the side of the cell that becomes concave in the case of unicellular plants and a similar aggregation in the cells of multicellular plants on the side that becomes concave. This accumulation of protoplasm on the concave side had been noticed by Ciesielski (5) and Sachs, who wrote (65, p. 221) that it was not the cause but the result of greater growth on the side becoming convex. Wortmann thought (80) the protoplasm accumulated in the cells of one side produced a thickening of the cell membranes on that side. This thickening retarded growth in the longitudinal direction, and as the growth on the opposite side was not retarded, the organ curved, the side with the thickened membranes becoming concave.

Elfving (19) and Noll (48) have shown that the difference in the thickness of the membranes appears only after the curve is formed; hence it cannot be the cause of the curve as Wortmann supposed. Also Noll's measurement of the membranes in curved grass nodes (48) shows that the membranes on the concave side are not at all thickened, or only slightly more than the normal, but those on the convex side are much thinner than normal. Noll found in unicellular plants, walls unequally thickened on opposite sides of the organ which did not curve as it must have done had Wortmann been correct.

In partial agreement with Wiesner, Noll believes the curve is produced by a change in the quality of the membranes, those on the side which is later convex becoming more extensible. He seeks to prove this point by his bending experiments. Stems that were just beginning to curve were subjected to a pull at right angles to their long axes in the plane of the curve just beginning. This pull was exerted by a given weight for a

definite time, alternately toward the convex and concave sides. They always bent farther toward the concave side, and the con clusion was drawn that the membranes were more extensible on the convex side.

Noll sometimes found a shortening of the concave side of curving stems of Hippuris of 6–10 per cent. He quotes some figures from Sachs which show a shortening of 10–25 per cent. in nodes of maize (**48,** p. 528). He does not believe in the migration of protoplasm required by Wortmann's theory, nor did the latter offer sufficient proof of it. In plasmolyzing experiments Noll discovered at the beginning of plasmolysis a slight increase of the curve, followed only later by the straightening which de Vries had found. This increase of the curve on plasmolyzing does not take place after the curve is complete. Kohl confirmed these observations (**33,** p. 70). In a later paper (**50,** p. 84) Noll admits that his theory of the curvature does not fully explain this plus curve.

Both Wortmann and Noll seemed to start out with the hope of showing that the factors which produce the curvature operate on only one side of the curving organ, Wortmann finding them on the concave, Noll on the convex side. Both men, however, were compelled either by their own discoveries or by their critics to admit at least secondary changes on the other side.

In 1894 another theory of the mechanism of growth-curvatures was presented by Kohl (**33**). It may be called the *contraction theory*, and is supposed to account for the shortening of the concave side of curving organs, which had been reported previously by a number of observers. As a starting point, Kohl accepts Kraus's results that during the curvature osmotic substances increase on the concave side, and those of Noll in which plasmolysis shows a slight relative increase of turgor on the concave side, and confirms these results by plasmolyzing experiments in which he found constantly, in organs that were in the early stage of the curve, the protoplasm contracted from the walls of the cells on the convex side sooner than in those on the concave. He also found by microscopic examination that there

was a larger amount of copper-reducing substance in the cells of the concave side. Unable to accept either Wortmann's or Noll's views as to the cause of the curvature, Kohl elaborated the theory that the curvature is caused by an active contraction on the concave side, with a corresponding passive stretching on the convex side. The possibility of this contraction depends upon the fact, which can be mathematically demonstrated, that an oblong cell may increase in volume, and at the same time shorten its long diameter. Of course, the transverse diameter must increase, and the cell become more nearly spherical. The force that produces this shortening is the increased turgor of the cell, which, beyond a certain point, makes the cell shorter and broader, or, as Kohl expresses it, barrel shaped. It is at once seen that a condition necessary to the contraction of an organ in this manner is that the cells must lie with their long diameter parallel to the long axis of the organ. This condition Kohl himself seems to have overlooked, and it will help us to determine whether his theory is applicable to given cases of curvature.

In discussing the theoretical possibility of producing a contraction by increased turgor Kohl attempts to show that the conditions are favorable to it in stems where there are large intercellular spaces. Here we have what he calls alternately single and double membranes, the latter where two cells are in direct contact, the former where the cells border on intercellular spaces. To make this more clear, he compares this condition to an India rubber cell (33, p. 8) on the outside of which thicker strips have been fastened longitudinally. Now, if the India rubber cell is filled with water under pressure, it will stretch more in the transverse than in the longitudinal direction, because of the thicker strips in the latter direction. Here again Kohl overlooked a condition which must exist in organs with intercellular spaces, namely, that where the membrane is double the stretching force is doubled also, for a cell on each side of the membrane is stretching it in a longitudinal direction. Kohl probably got his idea of the contraction theory from some experiments of de Vries (74) in which he found that many roots,

especially fleshy ones which have a very large proportion of parenchyma tissue, contract by the absorption of water. Kohl agrees with Noll that at the beginning of the curvature there is no measurable difference in the thickness of the cell walls on the two sides, and that as the curve progresses the difference comes rather by thinning of the convex membranes than by a thickening of the concave membranes. Hence Wortmann's view cannot be correct. This view does not provide for a contraction of the concave side, a fact observed by former experimenters and confirmed by Kohl. He finds in Pisum that the cells of the concave side may shorten 19.4 per cent. of their normal length. Noll's theory as first enunciated provides for the shortening of the concave side only by a passive compression, though, as modified later, it allows a greater elasticity of the walls on that side.

In further support of his theory Kohl cites the fact that grass nodes, in curving, often break on the convex side with transverse clefts. This could not take place if the curve was produced by a greater extensibility on that side. This counts against Noll's theory, but is in perfect harmony with Kohl's theory which makes the lengthening of the convex side wholly a passive stretching. He shows by measurements in both stems and roots that the cells of the concave side become shorter and broader, and that those of the convex side become longer and narrower than normal.

Kohl thinks his theory accounts for the plus curve observed by Noll, though I cannot see the force of his reasoning. If increased turgor contracts the cells, decreased turgor ought to expand them. Noll showed (50, pp. 49–50) that this is not the case.

In a series of experiments Kohl cut transverse notches 2^{mm} apart in stems to the depth of the vascular bundles, and laid them in a horizontal position, some with the notched side uppermost, others with the notched side downward. The latter always curved more rapidly than the former, but Noll has shown that the difference was due to the traumatropic effect of the cutting. It is an interesting and perhaps a significant fact that when these organs curved water was forced out of the notches.

Some experiments on tissue tensions showed that when curved stems of Pisum were split into two equal parts both parts curved outward, that is, the concave side curved more and the convex side straightened. If the stem is split in parallel planes into three parts the concave cortex shortens and the convex cortex and pith remain about the same length. Kohl implies, though he does not directly say, that the tissue tensions indicated by the result obtained were due to the stimulus. In a footnote to his preface Kohl says he regards the stimulation curvatures as merely phenomena of tissue tension. Yet in his book (33) he devotes less than three pages to tissue tensions, and in his discussion he is only half right because he ignores the tissue tensions existing previous to the application of the stimulus and independent of it.

Pfeffer (56) reports some very searching experiments on stimulated grass nodes, and incidentally gives his views on the mechanism of curvature. The anatomy of grass nodes is very different from that of curving roots and most stems. The curving takes place only in the cushion of the leaf sheath at the node. The middle tissue of the cushion consists of a hollow cylinder of vascular bundles accompanied by a very large amount of collenchyma. This cylinder is bounded both internally and externally by thin-walled parenchyma. The tissue tensions are such that the parenchyma, freed from the bundles, lengthens 30–40 per cent., while the bundles contract less than 1 per cent. In the process of curving, when the grass stems are placed in a horizontal position, the growing collenchyma on the lower side frees the parenchyma on that side from its positive tension, and may even put it under a negative tension to such a degree that it is frequently broken in transverse clefts to the depth of the bundle. Thus the passive stretching of the convex side which Kohl supposed was produced by the contraction of the concave side, proves to be due to the reversed tensions between two tissues, both of which are in the convex side (56, p. 407). This applies to grass nodes only. Pfeffer's results prove conclusively that the contraction theory cannot possibly account for the curve in grass nodes, and Wortmann's theory is even less adequate.

As for the increased extensibility of the membranes on the convex side by which Noll accounts for stimulation-curvatures, it undoubtedly exists, but in the collenchyma, and not in the parenchyma. The change in the quality of the membrane is inferred by Noll both from a difference in the optical properties of the membranes, and from their decreased thickness and greater superficial area. However it is almost beyond doubt that in grass nodes this change in the quality of the membranes is a phenomenon of growth and is not a simple process of stretching, either plastically or elastically (**56,** pp. 405, 416).

In 1897 J. Loeb published a paper (**36**) in which he accounted for geotropic and heliotropic curvatures by a contraction of the concave side, not in the sense of Kohl's contraction, but in the sense in which the term is used in animal physiology. The contraction in plants is exactly the same as the contraction of muscles. Loeb thinks his theory is of universal application. It not only explains all the stimulation-curvatures of plants both unicellular and multicellular, but also those of animals (marine worms and hydroid polyps) and even puts phototactic and chemotactic movements of motile organisms on the same basis as heliotropic and geotropic curvatures. Loeb's plea for a simple explanation which will apply to all cases of movements and curves caused by stimuli has been anticipated and answered by Pfeffer. He says (**56,** p. 413) : "The demand which is always recurring in relation to movements of curvature that the mechanics of the process be everywhere identical is only to be understood from the natural inclination to simplifying schemes, or from a narrow-minded view of living nature." Nature makes use of many means to accomplish similar ends. In its application to particular cases Loeb's theory is as inadequate to account for the curvature of grass stems as those of Wortmann and Kohl, and for the same reason, namely, it could not develop sufficient energy to accomplish the result, as Pfeffer's experiments prove (**56**). In the case of movements such as those performed by the pulvini of Mimosa and by sensitive stamens, water is given out into the intercellular spaces when the contraction takes place, and the shortened side

of the organ is not rigid but flaccid, while a contracting muscle takes up water (**36**, pp. 446, 447), and is more rigid than in the unstimulated condition.   Loeb's theoretical explanation as to how gravitation causes a curvature presupposes that gravitation acts directly on the cells concerned in the curve (**36,** p. 448). This is not the case, however, in roots where the tip only is sensitive to the stimulus, and the changes in the cells where the curve is produced are brought about by an influence transmitted from the tip.   The objections of Elfving and Noll to Wortmann's theory as applied to unicellular plants seem to me to be equally valid against the theory of Loeb for these plants.

An   article   on   root   curvature   was   published   by   D.   T. MacDougal in the BOTANICAL GAZETTE for May 1897.   Among other conclusions he has the following : "The curvature of roots is due to the excessive active elongation of the internal layers of the cortex, of the side becoming convex, made feasible by the increased stretching capacity of the longitudinal membranes. The extension of the membranes is accompanied or preceded by changes in the quality of the membranes as indicated by their reaction to staining fluids."   MacDougal believes, then, that the convex side is alone active in producing the curvature, and he supports his view by measurements of cells on both the concave and convex side of curved roots, which are compared with measurements of cells in straight roots.   The figures given show that, in the roots of *Zea Mais* curved geotropically 105°, the cells of the convex side are 3.2 times as long as those in the normal root, while the cells of the concave side are 2.1 times as long as the normal ones.   Not only does the convex side grow much faster than the normal root, but the concave side also is much accelerated in growth.   These results contradict the observations of several writers that the concave side often actually shortens, and indicate a rate of growth in stimulated roots which has not been observed by any other writer.   I can only conclude that the cells measured in the normal root did not correspond to those measured in the curved root.   The paper is obscure on the point as to how the author knew what cells to measure.

Apparently he took cells at equal distances from the tip in the normal and in the curved roots; but cells so situated would be comparable only if the two roots elongated at the same rate after the stimulation of the one, and this rate is just the point to be proved. To assume it, therefore, is to beg the question. MacDougal's results give further evidence that his "normal" roots were not normal. In his tables IX and X he gives results with roots bent mechanically, one after being geotropically excited one hour, the other without excitation. This latter one (table IX) must have been normal up to the time of bending, and as the author says the cells of the convex side have enlarged and those of the concave side diminished, the latter cells ought to be shorter than normal, but the figures given show the cells of the concave side in the root bent mechanically to be five times as long as the cells in his "normal" root. In the roots mechanically bent the curve of shortest radius coincides with that in roots geotropically excited; hence the latter are comparable to the former, taking into consideration the time element. If there is as much elongation in the region of greatest curvature of geotropically curved roots as MacDougal supposes, those which are geotropically excited and then bent mechanically ought to have longer cells than those bent without excitation, as both were bent 90°; but the figures show that cells on the concave side of roots stimulated before bending are little more than half as long as those bent without stimulation. Also the cells in the convex side of the former are only three fourths as long as those in the corresponding part of the latter. Looking at all the figures given by MacDougal, it is found that in all the roots curved geotropically the cells on the concave side are shorter than those on the same side of roots bent mechanically without stimulation; this is true even for the curves one hundred hours old, though here the growing tip has advanced 3^{cm} beyond the curve of greatest radius. Even the cells of the convex side of roots curved geotropically are shorter than those on the corresponding side of the roots bent mechanically, except in those curves which were seventy and one hundred hours old. So far from admitting

the correctness of MacDougal's conclusion, I am forced by a careful examination of his results to the view that roots geotropically stimulated shorten their cells on the concave side. This is shown even without taking his mechanically bent roots as the basis of comparison. Roots curved geotropically three hours through 60° have convex cells 43. 3° of the scale in length, concave cells 29.9°. Roots curved geotropically twenty hours through 105° have convex cells 48.05°, concave 24.7° of scale in length. Obviously, as the curve progresses, the cells of the concave side shorten 5.2° of the scale, the convex cells lengthen 4.7°. I am unable to explain the difference in the length of cells in the "normal" roots and those bent mechanically, as reported by MacDougal. So far as the paper makes it clear, they were supposed to be measured in corresponding regions. If the difference is due to individual variation it still vitiates MacDougal's conclusions. If it is due to the fact that the cells measured were not in corresponding regions, then the measurements in "normal" roots do not correspond to those in roots curved geotropically, for the author states distinctly (**39,** p. 346) that "The region of curvature artificially produced coincided with that of geotropically excited roots."

HISTORICAL SUMMARY.

In summing up the historical part of the question under consideration it is easily seen that no theory of the mechanism of the curvature yet advanced is satisfactory for all cases, and that the very different mechanical relations of tissues in different organs capable of curving make it extremely improbable that a single simple explanation will apply to all growth-curvatures. The causes of curvature as conceived in the different theories may be classified somewhat artificially as follows :

1. Difference in rate of growth on opposite sides of the organ. Sachs, Pfeffer (?).
2. Activity of protoplasm.
   a. By increased formation of osmotic substances on the concave side, accompanied by contraction. Kohl, Loeb.

  b. By increased formation of osmotic substances on the
   convex side, accompanied by extension. De Vries.
 3. Difference in the quality of cell membranes.
  a. Concave membranes thicker, more resistant. Wort-
   mann.
  b. Convex membranes thinner, more ductile. Wiesner,
   Noll, MacDougal.

To be sure, all the theories must go back ultimately to the
activity of protoplasm ; but there is a question whether any fac-
tors are concerned in the curvature which are not concerned in
ordinary growth, and whether the activity of the protoplasm is
manifested in a change in its own condition, a change in the cell
contents, or a change in the condition of the cell membrane.
The curvature of grass nodes can be explained only by an
increased growth of tissue on the convex side. Some contrac-
tion on the concave side is not excluded, but such contraction
could not possibly develop energy enough to curve the organ.
Plastic stretching on the convex side is also inadequate in grass
nodes. Indeed, the changes in quality of the membranes on the
convex side, which Noll has described, are similar to those which
Strasburger has shown take place in cells of Cladophora when a
new branch forms. Hence Noll's plastic stretching may be only
a phenomenon of growth, and not a condition peculiar to curving
organs. Increased growth on the convex side, however, will not
explain the shortening of the concave side which has been
reported by several observers. De Vries's view of increased
turgor on the convex side is not tenable.

Original experiments.

MATERIAL AND METHODS.

 In the following experiments a study was made of the
traumatropic curvature of roots, and the materials used were the
roots of *Vicia faba*, the broad or Windsor bean. Some of the
experiments involved a separation of different tissues, and this
species was chosen because of the large size of the roots, which
were, therefore, easily manipulated, and in which the liability to

error was reduced to a minimum. With smaller roots it would have been impossible to separate the different tissues from each other with a sufficient degree of accuracy to make the results reliable. The seeds were germinated in moist sawdust, and when the roots had attained a length of from 1–5^{cm} the seedlings were removed from the sawdust, and placed with the roots pro jecting into water through holes in a thin board, the holes being of such a size that the upper part of the root fitted snugly, and the root was held in a vertical position pointing downward. The temperature of the water was regulated only by the temperature of the laboratory where the experiments were carried on, and was generally from 15°–20°C. No attempt was made to keep the temperature constant, and during the nights of the colder part of the winter it probably fell as low as 10°C. or lower; but as nearly all the observations used were made the same day the experiments were started, the fall of the temperature at night can have no effect on the results. The experiments were made with the roots in water rather than in moist air or sawdust, because the stage of the curvature could be seen in water without removing them and perhaps subjecting them to other stimuli; and it was found by trial that the results were much more uniform in water than in moist air.

At the time of removing from the sawdust or after they had been in water for some time, the roots were branded on one side of the tip by means of a hot piece of metal. A warm stage was heated by means of an alcohol lamp, and the roots, held at an angle of 45° or less from the horizontal, were placed with their tips in contact with the hot stage for an instant. The roots were then put into water as described before. In from one to four hours after branding they begin to curve away from the side that was branded, and when the curve had progressed sufficiently they were ready for further observations or operations. Control roots were nearly always used, and in selecting them they were generally paired off with the branded ones, so that the two sets should be as nearly alike as possible in point of size and stage of development. Roots that at first were inclined to curve

spontaneously were rejected.   Further details in the treatment of the roots will be given in connection with the different experiments.

It will be necessary to understand the general anatomy of the root in the zone of growth.   At the extreme tip of the root is a very well developed root cap which extends back as a sheath surrounding the whole root for 5^{mm} or more.   Where the cap joins the tip of the root proper is the zone of initial cells or primary meristem.   From this meristem are derived by cell division all the cells of both the cap and root proper.   All the cells of the initial zone are completely filled with dense granular protoplasm.   A very short distance above the initial zone, 1^{mm} or more, may be distinguished a central or axial cylinder composing, approximately, one third of the diameter of the root; and this central strand is surrounded by a cylinder of cortical parenchyma, characterized by numerous large intercellular spaces.   These spaces are more conspicuous in the longitudinal than in the transverse direction, and may be followed very near to the initial zone.   In sections of living roots these spaces are shown by the presence of air. Outside of the cortical parenchyma is the dermatogen layer, one or more cells thick.   The cells of the dermatogen layer are more densely filled with protoplasm than the cortical layer, whose cells have a comparatively small amount of protoplasm, and a very large central vacuole.   The cortical cells often have a large amount of starch in them.   The outer layers of the axial cylinder are also densely filled with protoplasm and furnish the path along which the reserve food is brought from the cotyledons to the growing cells, as has been determined by experiment.

The cells of the initial zone are nearly isodiametric.   The portions of the cortex nearest the initial zone often have the radial diameter of cells longer than the diameter parallel to the root axis.

Finally, all the cells come to have their longer diameter parallel to the long axis of the root.   The cells of the axial cylinder elongate longitudinally much earlier than the cells of the cortex.

PATH OF TRANSMISSION OF STIMULUS.

As has already been stated, in these experiments it is regarded as settled that only the tip of the root is capable of receiving the stimulus, and that an impulse is transmitted from the tip to the zone of curvature which in the most typical cases has a region of maximum curvature from $3-5^{mm}$ from the tip. The whole zone of curvature is somewhat longer but seldom extends more than 8^{mm} from the tip at first. Afterward, by growth in length of the root, the curve may come to lie farther from the tip. Under favorable conditions the tip of the root may describe an arc of 90° in from three to four hours from the time of the branding; and in these cases, where the curve is rapid, it is found by careful measurement that the zone of maximum growth does not coincide with the zone of maximum curvature, but the latter lies nearer the tip than the former. Later, as the zone of maximum growth advances the two may coincide. These results confirm those of Weisner (**78**). The method used for ascertaining the path of transmission of the stimulus was suggested by Kohl's notch experiments on stems. The objection urged against his experiments, that the cutting itself acts as a stimulus, does not hold with roots, for as the tip alone is sensitive, cuts made back of the sensitive part do not appreciably stimulate it.

The method consisted in cutting off certain parts of the root before branding, and ascertaining whether the stimulus was transmitted in the part that was left, past the cut, or, to put it in another way, whether the root curved both above and below the cut.

In one set of experiments the root was cut with a sharp, thin bladed razor, in a plane exactly at right angles to the long axis, generally at a distance of from $2-3^{mm}$ from the tip, though sometimes from $3-4^{mm}$ from the tip. It was very noticeable that the nearer to the tip the cut was made the larger the number of responses to the stimulus in which the curve was on both sides of the cut or gash. In many of those in which the curve

did not extend above the gash there was a typical curve between the gash and the tip. The gashes were made deep enough to cut off the axial cylinder more or less completely, though as this could not be seen at the time of cutting, in many of the roots a small part of the axial strand must have been intact.

TABLE I.

ROOTS GASHED THROUGH AXIAL CYLINDER.

Date	Branded on opposite sides			Control, gashed but not branded	
	Distance of gash from tip	Roots used	Roots curved	Roots used	Roots curved
1896					
Nov. 7	2.5–3 ^{mm}	3	3		
10	2	4	2		
11	2	6	3		
12		8	6	8	I
14		4	0 ?		
17		17	7		
23		5	2		
26	3–4	8	3		
30		14	4		
Dec. 1		8	6		
2	3–4	7	3		
3	3–4	8	3		
4	3–4	8	I		
1897					
Mar. 18	2–3	8	6		
		108	49		

Table I shows the different lots in a series of experiments in which the gash was made through the axial cylinder and the roots were branded on the opposite side of the tip. In the second column the blank spaces mean that no record was made of the distance from the tip at which the gashes were made. In the fourth column the numbers show how many of the roots curved away from the brand both above and below the gash. Many more of them showed a traumatropic curve between the gash and the tip, and this was especially true of those in which the gash was made 3–4^{mm} from the tip. It may be objected that there are not enough control roots, but many of these lots were

observed at the same time as other sets, which will be shown in other tables, and these acted as control experiments for each other. For instance, those in which the brand was on the opposite side from the gash served as control for those in which the gash and brand were both on the same side.

A total of one hundred and eight roots were gashed in the manner indicated in the table, and branded on the opposite side of the tip. Whatever traumatropic effect the gash would have on the root would, in this case, work against that of the brand. Of these roots forty-nine, equal to 45.3 per cent. of the whole number, curved away from the brand both above and below the gash. These roots were tested in lots, the number varying from three to seventeen in each lot. The observations must be made within five or six hours after branding, for after that time some that have shown the curve more or less plainly begin to straighten, and after twenty-four hours a much smaller number will show the curve above the gash.

TABLE II.

ROOTS GASHED THROUGH AXIAL CYLINDER.

Date	Branded on same side			Control, gashed, not branded	
	Distance of gash from tip	Roots used	Roots curved	Roots used	Roots curved
1896					
Nov. 10	2^{mm}	5	I		
11		7	4	5	I
12		8	4		
13		5	0		
14		6	I		
16		12	9		
23		5	4		
25		11	5		
1897					
March 19	$2-3^{mm}$	9	4	9^2	8
20	$2-3^{mm}$	8	6	8	I
		76	38		

This table shows that 50 per cent. of the roots curved both above and below the gash, when the brand and gash were on the

[2] These nine were branded, but not gashed.

same side, about 5 per cent. more than when they were on opposite sides. It is possible that the gash in some cases was near enough to the receptive part to give a slight stimulus, whose effect was, added to that of the brand. Of the two lots marked "control" which were gashed, but not branded, one of the five showed a distinct but not great curve away from cut side, and in the lot of eight the one that curved away from the cut had the cut only 2^{mm} from tip.

TABLE III.

ROOTS GASHED IN CORTEX ONLY.

Date	Branded on gashed side			Control, gashed, not branded	
	Distance of gash from tip	Roots used	Roots curved	Roots used	Roots curved
Nov. 10		5	4	4	1
11	2^{mm}	7	1	5	0
7	$2.5-3^{mm}$	3	3	3	1
12		8	6	8	1?
28	$2-3^{mm}$	9	5		
		32	19	20	3

In these experiments, where a large part of the cortex and all the axial cylinder were left intact, 59.3 per cent. of the roots curved both above and below the gash. Taking from the three tables all the control roots that were gashed, but not branded, we have a total of forty-one roots, of which six showed a curve away from the cut. In a few of these cases it was somewhat doubtful whether the curve was really the effect of the wound or simply a spontaneous curve. But, considering them as due to the cut, we have 14.6 per cent. curving from the effect of the cut. This is a greater difference than is indicated by the two sets of experiments where effects of the cut and the effects of the brand worked with each other in one set and against each other in the other set.

TABLE IV.

ROOTS GASHED ALL AROUND IN CORTEX ONLY, AND BRANDED ON ONE SIDE OF THE TIP.

Date	Distance of gash from tip	Hours after branding	Roots used	Roots curved	Curved only below gash
1896					
Nov. 13		4	8	0	6
14		6	6	0	4
16		24	16	0	8
17		5	16	0	few
18	3–4^{mm}	7	6	1	5
20		7	9	0	7
23		6	12	2	8
25	2–3	6	10	7	2
26	3–4	5	9	4	3
28	4	4	10	1	8
28	2	24	9	3	3
30	2–3	5	8	4	1
Dec. 7	3–4	6	10	1	1
7	2	12	10	1	?
8	2	7	10	3	0
8	3–4	10	10	2	7
10	2–3	6	10	3	1
10	3–4	6	10	0	7
15	2–3	11	20	4	3
17	2–3	7	20	7	0
1897					
March 17	2–3	4	6	3	1
			225	46 20.4%	76 33.7%

In this table the third column indicates the number of hours after branding when the observations here recorded were made. These were not necessarily the only observations, as with nearly all lots several observations were made at intervals of two or three hours, then again after twenty-four hours. In making up the tables those results were taken which showed the largest number curved. The column headed "roots curved" shows the number that curved both above and below the gash. The last column shows the number that curved between the gash and the tip in addition to those in the preceding column.

It is seen that in these roots in which the cortex is cut off as completely as possible only 20.4 per cent. of the roots curve, though the axial cylinder was practically all present. Owing to

the impossibility of cutting exactly to the required depth, small parts of the cortex were probably left in many of the roots. Putting together the results of the last two columns, we see that more than 50 per cent. of the roots curved in some degree away from the brand. Hence the cutting did not inhibit the curvature as might be objected, but kept it below the cut in the large majority of cases.

TABLE V.

AXIAL CYLINDER OF ROOTS CUT OFF BY STABBING.

Date	Branded on same side as stab		Branded on side opposite to stab		Branded on side 90° from stab	
1896						
Nov. 16					16	2
17					16	3
18					7	5
19			11	8		
20	12	0	10	3		
21			10	6		
21	9	5	10	8		
21			9	6		
23			7	5	13	12
24					9	7
24	9	9			9	7
25					9	5
27			9	9	9	6
Dec. 7					10	7
7					10	4
9					10	7
9					10	3
15					20	10
17					20	14
1897						
March 13					9	6
15					14	11
16					17	16
	30	14	66	45	208	125
		46.6 %		68.1 %		60.0 %

Table V is instructive as evidence on the question of the transmission of the stimulus. All the roots had the axial cylinder cut off as completely as possible, in such a way as to leave as much of the cortex as possible. The cutting was done with a long slender pointed scalpel, so narrow that it could be pushed through the root, cutting off the axial cylinder, but leaving most

of the cortex intact on two opposite sides. Some of the cortex necessarily had to be cut in getting to the axis, especially on the side where the scalpel was pushed in. A small amount of cortex was also cut on the side opposite to this, for the scalpel had to be pushed through till its point could be felt on the farther side. Part of these roots were branded on the side from which the scalpel was pushed in, part of them on the side opposite, and part of them 90° from that side. A total of 304 roots were used, and of these 184 curved away from brand both above and below the stab in the root. That is, 60.5 per cent. showed the typical traumatropic curve more or less distinctly.

The lot of sixteen tested November 16 was not looked at after branding for twenty-four hours, or the result might have been different. I cannot explain satisfactorily the low result on November 17 and 20, unless the stab was made too far from the tip. In most of the lots the stab was made between 2 and 3^{mm} from the tip, and the roots were looked at several times within the first eight hours after branding as well as twenty-four hours after. The results were taken when they showed the greatest number curved. The necessity of control experiments in which the roots should be stabbed and not branded, was obviated by branding on different sides as related to the position of the stab. Thirty-six control roots were branded, but not stabbed, and twenty-nine of them curved away from the brand, 80.5 per cent. In roots branded under the most favorable conditions only about 5 per cent. fail to show the traumatropic curve.

In order to be certain that the stimulus was not transmitted in parts of the axial cylinder which might not have been cut off, many of them were afterward examined microscopically. In an especially favorable lot of seventeen roots, of which sixteen showed the traumatropic curve both above and below the stab, twelve of them had the axial cylinder completely cut off, and those that had the axial cylinder partially intact were among those that curved least and straightened soonest.

Six hours from the time of branding some of the roots that had curved somewhat were already beginning to straighten.

The stabbed ones did not curve so much as the control, and a larger percentage of them straightened within twenty-four hours. A possible source of error is seen here, since, if observations are not made within a few hours after branding, the root may have already curved and straightened. This may account for the negative results in some of the earlier lots.

If we leave out the first two lots of sixteen roots each in which the results are so low, we get exactly the same percentage of curved roots, 68.1 per cent., in both those that were branded on the side opposite to the stab and those that were branded on the side 90° from the stab. This is only 11.9 per cent. less than the control roots which were branded and not stabbed. This difference might easily be due to the inhibiting or paralyzing action of the injury.

Putting together the results of these experiments, it is seen that the transmission of the stimulus past the cut depends very largely on how much of the cortex is present. The lowest percentage of curved roots (20.4 per cent.) was found in those that had the axis complete, but much of the cortex cut off (table IV). The highest percentage of curved roots, 60 per cent. and 68.1 per cent., was found among those in which the axis was completely cut off, but the cortex mostly present (table V). The results in tables I, II, and III show a curving in proportion, roughly speaking, to the amount of cortex present. When the axis, as well as a large part of the cortex, was left intact 59.3 per cent. curved on both sides of the cut, only 1.2 per cent. less than when the axis was cut off completely.

We are therefore justified in drawing the following conclusions :

1. The stimulus can be, and is, transmitted in the cortex.

2. While it is not absolutely demonstrated that the impulse cannot be transmitted in the axial cylinder, it seems very probable that it is not transmitted there.

3. The impulse that affects the part of the root above the cut can be transmitted in the cortex of either the concave or the convex side.

4. The stimulus can also be transmitted transversely, or at least tangentially in the cortex. This follows from the fact that the curve was formed when only a small part of the cortex was left either on the concave or convex side. The stimulus, after passing the cut on one side, still influenced the cells on the opposite side to aid the curve.[3] This is a fact which every theory of curvature must take into consideration.

5. The experiments in table II disprove Wiesner's theory of the traumatropic curvature of roots. He says decapitation of the root tip accelerates growth in the region of the curve by making the walls more ductile. Injury to one side of the tip increases the ductility of the membranes on that side of the root; hence it grows faster than the other and the curve results (**78,** p. 268). If Wiesner's view were correct the gash on the same side of the root as the brand would prevent any curve above the gash; since neither the stimulus nor any tensile strain could be transmitted across the cut. As the root does curve above the gash Wiesner's view cannot be correct. The process is more complicated than he supposed.

6. These results seem to show that both sides are concerned in the formation of the curvature, certainly to the extent of conducting the stimulus, and if to that extent probably both sides are also concerned in the changes in the cells that produce the curve directly. This point will be discussed more fully later.

TISSUE TENSIONS.

It has long been known that the pith of dicotyledonous stems grows faster than the cortex, and that as a consequence there is considerable tension between these tissues. The pith is under positive, the cortex under negative tension, so that when the stem is split in the growing part the two halves bend outward, the cortical side becoming concave, the pith side convex. In the normal stem the tensions between the pith and the cortex of any

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[3] Czapek (7) has recently shown, by the same method that I have used, that the stimulus can be transmitted in a transverse direction in roots. A *résumé* of my own experiments was first published in the Proceedings of the American Association for the Advancement of Science for 1897.

side tend to curve the stem toward that side. But this is bal-
anced by an equal tendency on the opposite side to curve in the
opposite direction, and the stem remains straight. The poten-
tial energy of this normal tension is available for producing a
curve as soon as the equilibrium of tension is disturbed. This
equilibrium may be disturbed either by an increase of tension on
one side, in which case that side will become concave, or by a
decrease of tension on one side, in which case that side will
become convex, or both these changes may occur. Kohl (33,
p. 87) thinks the first of these alternatives is the true one,
because when a curved stem is split in halves the convex half
straightens or curves in the direction opposite to that of the
whole stem. Kohl does not make sufficient allowance for the
tissue tensions which are present previous to stimulation. The
convex half of the curved stem will curve more in the original
direction when separated from the other half, only in the case
in which the tension on the convex side is reversed from the
normal, that is, where the cortex becomes longer than the pith.
This probably seldom happens. Kohl's experiments taken with
those of Sachs (63), in which curved stems were separated into
three strips, concave cortex, pith, and convex cortex, show very
conclusively that the stimulus influences the tension *on both sides of
the curving stems*, and that the tension is decreased on the con-
vex side, and increased on the concave side. Sachs' experi-
ments also show that the deviation from the normal is greater on
the concave side than on the convex side, that is, the increase of
tension on the concave side is greater than the decrease on the
convex side. These tension relations explain the results of Noll's
bending experiments, from which he draws the conclusion that
the membranes of the convex side are more extensible than
those of the concave side, because the stems bend more easily
toward the latter side. However, increased tension between the
pith and cortex of the side becoming concave, even without the
decreased tension on the opposite side, causes a greater resist-
ance to bending toward the convex side than toward the con-
cave. Hence Noll's conclusion does not at all follow from his

results. Without at present going into the question as to how stimuli cause the changes in tensions of normal stems, it seems very certain that changes of an opposite kind are produced on opposite sides of curving stems. Those writers, therefore, who attempt to explain stimulation-curvatures by a change on only one side of the curving organ are overworking a half truth.

On taking up the study of roots the question presents itself as to what the tissue tensions of roots are and how stimuli affect them. Hofmeister asserted that there were no tissue tensions in roots. More recently Pfeffer has written (**53**, p. 31): "In the zone of roots in which growth in length takes place, in spite of differentiation of tissue, only a slight longitudinal tension is shown." . . . . "A certain negative tension is to be assumed for that part of the axial vascular cylinder which is still capable of growth, since a gradual curve results with the concavity toward this part, if a root split longitudinally is kept under proper conditions." Pfeffer refers to the experiments of Sachs (**62**, p. 435) for the truth of his statement. My own experiments lead me to believe that the tissue tensions of roots are more important than has been supposed, and that they play a considerable part in the formation of curvatures. That the tension between the axial cylinder and cortical parenchyma in roots can become considerable is shown by the fact that in *Vicia faba* roots growing rapidly in water the axial cylinder is frequently ruptured transversely by the more rapidly growing cortex. These breaks in the axial cylinder become visible only when the root is cut into longitudinal sections, and I have found as many as six breaks in the same root within a piece of the root 2–3^{cm} long. Besides the method used by Sachs to show tissue tensions of roots, namely, splitting them into longitudinal halves, I have also used the method he and others have applied to stems. If the cortex is carefully separated from the axial cylinder and the separated lamellae left attached to that part of the root above the zone of separation, the lamellae of the cortex project beyond the axial cylinder. If the tip of the root is cut off square before the separation, the difference in length after separation becomes visible

to the unaided eye, and usually may be measured with an ordinary millimeter scale. A root of *Vicia faba* whose total length was 1.5^{mm} had its cortex separated from the axial cylinder in the zone of growth, and immediately afterward was laid in water. After ten minutes the isolated strips of cortex were 9^{mm} long, and the axial cylinder was 8^{mm} in length, a difference of 12.5 per cent. computed on the length of the axial cylinder. To compare this difference with that found in stems we may take the figures given in Sachs's *Text-book*, English edition, pp. 798–9, where the greatest difference in length of pith and epidermis of stems of *Silphium perfoliatum* is 13.4 per cent. This would probably have been somewhat greater had the pith and epidemis been separated from each other. Nevertheless the comparison shows that the amount of difference in the length of isolated tissues of roots may approach that of stems. It does not follow that the tissue tensions in the growing zone of roots represent as much potential energy as those of stems. The resistance of the tissue under negative tension in roots is much less than that of the tissue under the same tension in stems, and for the reason that the vascular bundles are so incompletely developed in the growing zone of roots. This explains why the axial cylinder of roots is often broken by the negative tension to which it is subjected, and also why the halves of split roots do not always curve with the cut face concave immediately after splitting. This curve always follows sooner or later provided the halves continue to grow, except when the root is laid in a horizontal position with the cut face upward. Often in roots growing rapidly the curve follows at once after splitting.

The root on which the above measurements were made was afterward plasmolyzed in 10 per cent. KNO_3. The cortex shortened 1^{mm}, the axial cylinder, 0.5^{mm}. In some cases the axial cylinder shortens more than the cortex, a fact which the tables do not show. The fact that the axial cylinder is shorter than the cortex after plasmolysis proves that the difference in length is not due merely to turgor, but that there is normally a difference in the rate of growth of the two tissues.

The separation of the cortex from the axial cylinder was done by first cutting off the cortex with a sharp razor on two opposite sides, in to the axial cylinder, for a distance from the tip equal to the length of the growing zone. This left a lamella of the root consisting of the axial cylinder, with a narrow strip of cortex on two opposite sides. Then 1^{mm} of the tip was cut off exactly transversely. With a very fine-pointed, thin scalpel the strips of cortex were separated from each other, but all left attached to the upper part of the root. The separation can be made quite accurately with roots as large as those of *Vicia faba*. The operation left the strips of tissue free to curve or straighten, lengthen or shorten. The time required to perform the operation was two or three minutes, and the roots were dipped in water several times during the operation to prevent wilting. After the separation they were laid in water and were observed for changes during several minutes.

TABLE VI.

POSITIVE TENSION OF CORTEX IN STRAIGHT ROOTS AS SHOWN BY DIFFERENCE IN LENGTH ON FREEING FROM AXIAL CYLINDER.

	In water				In KNO₃ 10%			
Date 1897	Roots used	Cortex longer than axis	Cortex shorter than axis	Cortex and axis equal	Roots used	Cortex longer than axis	Cortex shorter than axis	Cortex equal to axis
January ?	8	7		1				
March 29	10	5	1	4	9	6	2	1
March 30	10	5	2	3	7	6		1
April 20	16	15		1	15	13		2
	44	32	3	9	31	25	2	4
		72.7%	6.8%	20.5%		80.6%	6.5%	13%

In these experiments the roots were observed especially for the difference in length between the cortex and axial cylinder after the strips were separated from each other. Forty-four roots were observed in water, and thirty-one of these were plasmolyzed in 10 per cent. KNO_3. In almost three fourths of the roots the cortex was longer than the axial cylinder when they were placed

in water, and on complete plasmolysis a still larger proportion showed the cortex longer than the axial cylinder. This difference in length was often greater in the same root after plasmolysis than before. The observations were made with the unaided eye or with a lens of about ten diameters. Even though there was a small number of roots in which the cortex was under negative tension, it is clear from the table that in the large majority of cases the cortex is under positive tension and the axial cylinder under negative tension.

A series of experiments designed to ascertain the effect of stimulation on tissue tensions, as indicated by difference in length of separated tissues, is shown in table VII.

TABLE VII.

EFFECTS OF STIMULATION ON TENSION.

Date 1897	Roots used	x longer than v, v longer than a	$x=v$, both longer than a	x longer than a, v shorter than a	x longer than a, $v=a$	$x=a$, v shorter than a	x shorter than a, v shorter than x	
January 16	I	I						
April 20	22	6	2	5	8			
March 30	7		2	4	I		I	In water
	30	7	4	9	9		I	
		23.3%	13.3%	30%	30%		3.3%	
January ?	2			I		I	$x=v$ both$=a$	In 10% KNO₃
March 30	6	2	I	3		I	2	
April 20	23	9	2	4	3	3	2	
	31	11	3	8	3	4	2	
		35.5%	9.6%	25.8%	9.6%	12.9%	6.4%	

In these experiments the roots were branded and as soon as they began to curve, or while the curve was in progress, they were sliced and split as before in such a way that the three strips of concave cortex, axis, and convex cortex lay in the plane

of the curve.   In the table x stands for the strip of convex cortex, v for concave cortex, a for the axial cylinder.   The first part of the table shows the relative length of x, v, and a in water, the second part in 10 per cent. KNO_3.   Sometimes the cortex curved away from the axis, and had to be held in place in order to see their relative length.   In doing this care was taken not to push the axis out of the position it naturally took.   Most of the roots were somewhat curved, and if they were forcibly straightened, x was always longer than a, and v nearly always shorter than a.   The time of splitting varied from 1.5–6 hours after branding.

From the table it is seen that in water 23.3 per cent. and in KNO_3 35.5 per cent. of the roots showed both strips of cortex longer than axis and the convex side longer than the concave. In 13.3 per cent. of those in water and 9.6 per cent. of those in KNO_3, x and v were equal but both longer than a.   In water x was shorter than a in 3.3 per cent., in KNO_3 x was equal to a in 6.4 per cent. of the roots.

In water x was longer than v in 86.6 per cent. and longer than a in 96.7 per cent. ; v was longer than a in 36.6 per cent., equal to a in 30 per cent., and shorter than a in 33.3 per cent. of the roots.

In KNO_3 x was longer than a in 80.5 per cent., and longer than v in 83.8 per cent.; v was longer than a in 45.1 per cent., equal to a in 16 per cent., and shorter than a in 38.7 per cent. of the roots.

All the measurements in this table are merely relative and not absolute.   It is not shown from these experiments that the tension is increased on the convex side, but it is shown beyond a doubt that it is decreased on the concave side to such an extent that in about one third of the cases it was reduced to zero, and in another third was reversed, the cortex of this side becoming negative with respect to the axis.   This shortening cannot be merely by compression, for there is not sufficient lengthening of the convex side above the normal to account for so much compression.   Hence the stimulus causes a change in the cells of

the concave side that at least prevents them from lengthening in proportion to the axis and the convex cortex.

TABLE VIII.

ROOTS BRANDED AND SPLIT INTO HALVES AFTER CURVE HAS BEGUN.

Date 1897	Roots used	Hours after splitting	z and y curved in	z curved in, y out	z curved in, y straight	Both z and y straight
Jan. 27	3	4	1		2	
28	6	1.5	1	5		
29	4	1		1	3	
30	5	0.5		1	4	
Feb. 1	11	2.5	6	1	2	2
2	7	1.5	2	4	1	
3	3	1.5		1	2	
4	5	4	3		2	
5	5	3	1	4		
8	5	1.25		5		
9	6	5	1	4	1	
10	10	2		3	4	2
	69		15	29	21	4
			21.7 %	42 %	30.4 %	5.8 %

In the experiments shown in this table, the roots were branded and placed in water until the curving had begun. They were then split into two equal parts by means of a sharp thin scalpel, in such a manner that one half was the convex side and the other the concave side. The branding was done at such a point that when the roots were split completely one cotyledon remained attached to each half, so each half could get its supply of materials for growth. The halves were separated from each other completely, and the half roots were all placed in water in an upright position. By *curving in* is meant that the tip of the half root turned toward the cut face. *Curving out* means that the tip of the half root turned away from the cut face. The letter z stands for the convex half, the letter y for the concave half of the curve that was due to the branding. The two halves of the same root were kept so that they were compared with each other, and the numbers in the right hand column of the table stand for whole roots, the two halves of which behaved as

indicated at the top of the column. The discussion of this table will be taken up in connection with tables IX and X.

TABLE IX. CONTROL FOR TABLE VIII.

STRAIGHT UNINJURED ROOTS SPLIT INTO HALVES AT THE SAME TIME AS SOME OF THE BRANDED ONES.

Date 1897	Roots used	Hours after splitting	Both halves straight	Both curved in	Both curved out	One in, one out	One straight, one out	One straight, one in
Jan. 27	3	3.5	1		2			
28	4	1.5		2		2		
29	3	1		3				
29	4	2.5	1	2			1	
30	5	0.5		2				3
Feb. 1	5	2.5	1	2				2
2	4	1.5	3				1	
3	3	1.5	3					
4	3	4		3				
5	5	3		5				
8	4	1.25	1			3		
Apr. 13	8	6		8				
	51		10	27	2	5	2	5
			19.6%	52.9%	3.9%	9.8%	3.9%	9.8%

This table shows the results with roots which were straight and not branded, but which were split at the same time as branded roots shown in tables VIII and X. The lots that are directly comparable may be known by looking at the date and the column showing the hours after splitting at which the observations were made. Thus all the lots in table IX, except one on January 29 and one on February 4, may be compared with lots in table VIII.

It will be seen that 52.9 per cent. of the roots shown in table IX had both halves of each root curved in toward the cut face at the time the record was taken for the table. Sooner or later all the halves that grew at all, curved in this way. This latter fact the table does not show. The different series may be compared in several ways to show the effect of the branding ; first, as to the number of roots that show a given curve at a given time ; second, as to the extent of this curve ; third, as to the

time at which the curve begins. The first and third of these are the only comparisons that can be made from the tables. The second will be shown by a diagram.

TABLE X.

ROOTS SPLIT INTO HALVES AND AFTERWARD BOTH HALVES BRANDED ON OUTER SIDE OF TIP.

Date 1897	Roots used	Hours after branding	Both halves curved in	One straight, one curved in	Both straight
Jan. 27	2	3.5	1	1	
29	4	2.5	4		
Feb. 3	3	1.5	1	1	1
4	5	4	5		
5	5	3	3	2	
Apr. 13	8	6	8		
	27		22	4	1
			81.4%	14 8%	3.8%

It may be objected that these tables are not comparable because the time element is not constant. This objection is met by the fact that if we take table IX for the control of both VIII and X we have the time element varying similarly in the different tables. With a few exceptions the lots of the same date were under exactly the same conditions including the time element. Leaving out the exceptions and taking only those lots that were under the same conditions in all particulars, we get a different numerical result, but the general showing of the tables is the same. The numerical change is this : 69.2 per cent. of the roots treated as in table IX correspond to 81.4 per cent. of those treated as in table X. These had both halves curved in toward the cut face. Also 42.4 per cent. of the roots in table IX correspond to 19.0 per cent. of those in table VIII. These also had both halves curved in.

Making due allowance for the variation of the time element a number of facts become apparent. In roots that have begun to curve when they are split, the half nearest to the brand, the

convex side, goes on with its curving as rapidly as, or more rapidly than, the whole root would have done. The opposite half, the one that would have become concave in the whole root, may also curve more than at the time of splitting, but this curving is not invariable. This half may remain stationary for some time, then begin to curve toward the cut face, and therefore toward the brand. This curving in, however, has been delayed by the branding and only 19 per cent. of these roots have both halves curved in at a time when 42.4 per cent. of the control roots have both halves curved in. In the time that 69.2 per cent. of the control roots show both halves curved in, 81.4 per cent. of those that were branded on outer side of both halves show the same condition. Obviously, then, branding increases the rapidity of the curving of the convex half of the root. The other half of the root usually does not continue the curving away from the brand, but it is considerably delayed in curving in toward the cut face, which nearly always takes place sooner or later in both control and branded roots. These facts, on first thought, seem to indicate that only the convex side is active in producing the curve of the whole root. That does not follow, however, when it is remembered what the tensions of the root are previous to stimulation. The concave half of the root when separated will curve outward only when the stimulus has reversed the tensions on that side and put the cortex under negative tension in relation to the axial cylinder. If the tension were originally at the maximum for roots it could be considerably decreased on the concave side, and yet that half of the root could curve toward the cut face when separated from the other half. The fact that the concave half of the root sometimes curves farther, after separation, in the direction of the curve of the whole root, shows undoubtedly that the tension is sometimes reversed. In the cases in which the separated concave half curves no farther outward, the delay in curving with the cut face concave indicates that the original tension on the concave side was decreased but not reversed by the stimulus. Further experiments will be offered on this point.

In comparing split roots, both halves of which have been branded on the outer side of the tip, with control roots that have likewise been split but not branded, a notable difference is seen after a few hours from the time of branding both in the localization and the amount of the curve. *Fig. 1* shows this difference, *a* being a half root that was not branded, and *b* one that was branded on the outer side of tip. These curves were projected directly on paper, and show about the average condition in a set of sixteen roots, all of which were split throughout the length, with a cotyledon attached to each half root. The half roots were paired with their original fellows, and eight roots had both halves branded on the outer

Fig. 1.

side of the tip; eight were not branded. Six hours after splitting all the branded half roots except one are curved more than 90°, and the curve is localized in the region in which the traumatropic curvature takes place. Only five half roots out of sixteen not branded had curved as much as 90°, and the curve extended over a longer zone of the root. In these roots there was no difference in the time after splitting at which the curving began. This is only one set out of a number which showed the same general result. This result shows conclusively that the stimulus increases the tissue tension on the convex side of roots in the zone in which the traumatropic curvature is produced.
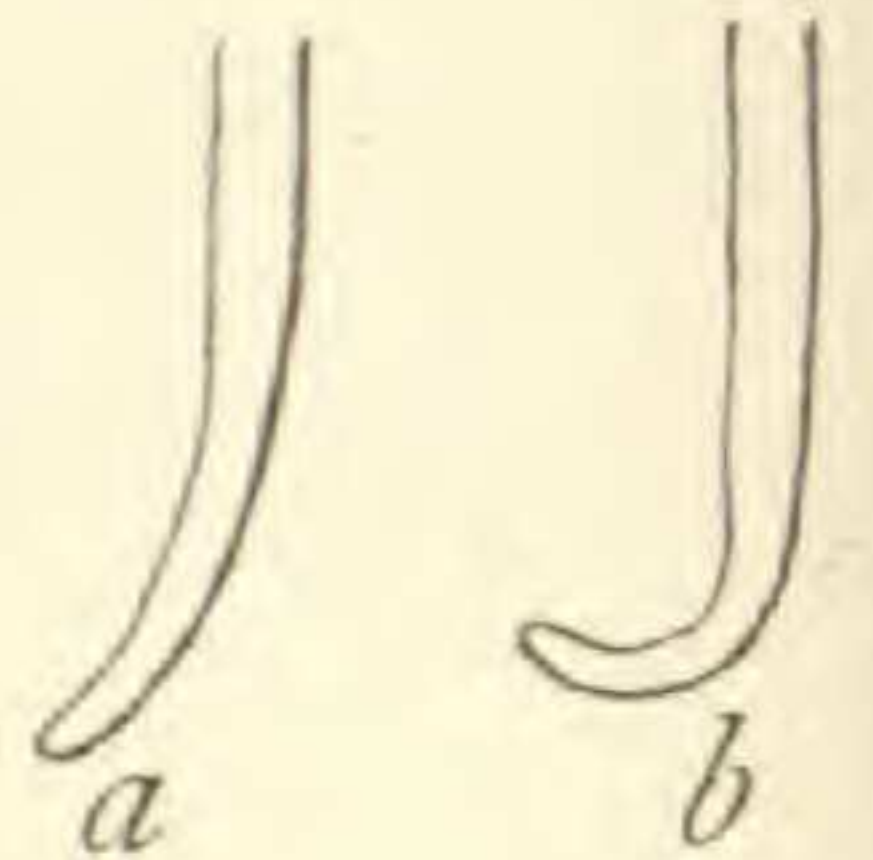
In the experiments shown in table XI roots were used that were already curved from branding, but in which the curve was still progressing, and in which, therefore, the conditions that bring about the curvature were still present. The roots were split at a time after branding which is indicated in the second column. The roots were sliced and split according to the method employed for table VII, and the three strips of convex cortex, axial cylinder, and concave cortex were observed with special attention to the curving of the parts after separation. The lettering is the same: x stands for the convex cortex, v for the concave cortex, and a for the axial cylinder. In a comparatively large number of cases both x and v pull away from a, x straightening

and v curving more strongly, but it was very noticeable that v pulled much farther away from a than x did, often forming a half-circle or more, and doing this with a sudden jerk as soon as it was free to do so. In other cases x lay up close to a, as before separation. These two cases are combined in column four, which shows the number, 55.8 per cent., in which v pulled farther away from a than x did. In this column x may either have pulled away from a or not.

TABLE XI.

MEDIAN SLICE OF CURVED ROOTS SPLIT INTO THREE STRIPS, CONVEX CORTEX, CONCAVE CORTEX, AND AXIAL CYLINDER.

Date. 1897	Hours after branding	Roots used.	v curves from a more than x	v and x curve more than at first	x curves from a more than v	x and v curve equally from a
Jan. 13	2	1	1			
14	2–4	6	4		1	1
15	3–4	3	1	1	1	
16	2–3	5	4			1
18	4	5	5			
19	2–4	6	3	3		
19	7	2	2			
20	2–3	2	2			
March 29	4–6	6	2	4		
30	4	7		7		
		43	24	15	2	2
			55.8%	34.8%	4.7%	4.7%

In the fifth column is shown the number of roots in which both x and v, after separation from a, increased their curve in the direction of that of the whole root; 34.8 per cent. of the total did this, though only four different lots showed it at all. Only a very small number showed x pulling away from a more than v, or x and v standing at equal distances from a. These experiments show that, aside from the difference in tension between cortex and axial cylinder the stimulus may also cause such a tension within the cortex of either side that it tends to curve away from the brand when completely free from other tissues. The next table will show that there is no such tendency in roots not wounded at one side of the tip.

It might be supposed that there was a contradiction between the results of table XI and those of former tables. Here we find the concave cortex showing a stronger tendency to curve than the convex cortex, but in the former tables we found that on splitting curving roots into two equal parts only the convex half continued the curvature away from the branded side, while the concave half usually remained stationary for a time and then curved in toward the cut face and toward the branded side. This, however, is easily understood through the tissue tensions. Since the cortex with ordinary growth tends to lengthen much faster than the axial cylinder, the cortex of the concave side might lose much of its positive tension and still be longer than the axial cylinder. The decreased tension on the concave side would allow the tension of the convex side to curve the whole root, even if the tension on the convex side did not increase. But if, under these circumstances, the root was split into halves, the concave half would stop curving, and if the tension on the concave side had not been neutralized or reversed, this half could even reverse its curve ; that is, curve in toward the cut face.

Table XI alone might seem to show that the concave side was the more active in producing the curve. We could not escape this conclusion if the curve were produced by the aggregate of the tendency of each individual tissue to curve. But recalling what we know of previously existing tissue tensions, we find it in complete harmony with the conclusion previously arrived at, that the stimulus diminishes tension on the concave side, and increases it on the convex side. Table XI especially confirms the view that the tension on the concave side is diminished, as well as changed otherwise.

It is possible, however, that the cortex of straight uninjured roots has a tendency to curve more or less regularly one way or another. Table XII will show that this is not the case.

This table is designed as control for XI. The roots were not branded, and were sliced in the same way as those in table XI. Since there was no curve the plane in which the three strips lie was not constant in relation to the seedling. In

comparatively few of these roots did one side of the cortex pull away from the axis more than the other. Eighty-two and nine tenths per cent. of them kept the same relative positions with respect to the axis. In many cases the two parts of the cortex lay up close to the axis, both remaining straight. In others the two parts pull away from the axis at the tip, though they seldom curved away from it very much. The axis always remains straight. From this table it is seen that there is no tendency in the cortex of straight unstimulated roots to curve as the cortex of stimulated roots curves. We are justified, therefore, in the conclusion that stimulation is the cause of the curving effects in the latter, when the cortex is freed from the axial cylinder.

TABLE XII.

MEDIAN SLICE OF STRAIGHT ROOTS SPLIT INTO THREE STRIPS.

	In Water			In 10% KNO_3		
Date, 1897	Roots used	One side curves more than other	Both sides curve equally from axis	All parts lie up close together	Both sides stand out equally from axis	One side stands out, other lies close to axis
Jan. 14	5	1	4	3	2	
15	3	1	2	2	1	
19	6	4	2	2	1	3
20	1		1	1		
Mch. 20	10		10			
30	10		10			
	35	6	29	8	4	3
		17.1%	82.9%	53.3%	26.7%	20%

The second part of table XII shows the effect of plasmolysis on some of the roots used. The first two columns of that part show that, in 80 per cent. of the roots tested for this particular effect, there was no difference in the tendency of the cortex on opposite sides of the same root to curve away from the axis when completely plasmolyzed.

In these experiments was first observed a very interesting phenomenon. When a root with the three strips free to move independently is put into 10 per cent. of KNO_3, the two strips

of cortex often curve far out from the axis, then rapidly come back up to it. The movement takes place within a few seconds and can be followed by the unaided eye. Whether the cortex spreads or not, almost without exception, so far as the observations went, the two strips of cortex at first became considerably shorter than the axis. The latter shortens much more slowly than the former, but after five minutes it has become shorter than the cortex and so remains.

I can think of two reasons why the cortex plasmolyzes more rapidly than the axial cylinder. The many intercellular spaces in the cortex allow the plasmolyzing agent to reach the cells more rapidly in this tissue. At the same time the abundant protoplasm in the cells of the axial cylinder may offer a greater resistance to the exosmosis of water than the thin layer of protoplasm in the cortical cells.

TABLE XIII.

MEASUREMENTS OF CURVING ROOTS.

First half cm. of concave side.

Date 1897	Roots used	Became longer	Did not lengthen	Shortened
March 20	5	2	2	1
24	3	2	1	
25	5	2	2	1
April 16	6		5	1
17	6	5	1	
	25	11	11	3
		44 %	44 %	12 %

This table shows that there is not merely a relative shortening of the concave side, but in almost half of the roots tested there was no growth in length at all on the concave side in the first 0.5^{cm} from tip, and in 12 per cent. there was an actual shortening in that part.

The roots were marked off with India ink, some in 1^{mm} spaces, some in 0.5^{cm}, and then branded. After the curve had made some progress they were measured again. The time varied from two to seven hours after branding, according to the

rapidity with which the curve took place. Only the first 0.5^{cm} was taken, because within the time stated the curve is confined almost exclusively to that region of the root. By taking the average of the roots tested, it was found that there is a greater difference between the lengthening of the concave side and that of normal straight roots, under the same conditions, than between the lengthening of the convex side and that of normal roots. In other words, the relative shortening of the concave side is greater than the relative lengthening of the convex side. This is further evidence against the supposition that the concave side is merely compressed. It has previously been mentioned that numerous observers have found a shortening of the concave side in stems of both monocotyledonous and dicotyledonous plants.

In the early stages of the curvature the zone of maximum curvature does not coincide with the zone of maximum growth. Indeed the curve may be completed before the two coincide. This fact had been frequently noticed in many experiments, and twelve roots were observed with this especially in mind. From four to seven hours after branding, ten of the twelve showed the curve almost wholly in the first 0.5^{cm}, while the maximum growth of these same roots was in the second 0.5^{cm} from tip. Of thirty-one straight roots carefully measured, the two measurements being four hours apart in most of them, four showed a greater growth in the 0.5^{cm} nearest the tip, twenty in the second 0.5^{cm} from the tip, and seven grew the same in both half centimeters. Within twenty four hours of the time of branding, however, if growth continues, the zone of maximum growth meets the zone of maximum curvature and finally passes it. I suspect, but have not proved, that this is the time when many of the curved roots tend to straighten. These results agree with those of Wiesner (**78,** p. 233).

RELATION OF CONCAVE CORTEX AND AXIAL CYLINDER.

A few roots were bent forcibly with the hand for about ten minutes and after lying a few minutes free in water they were

sliced into the three strips as before. A considerable curve remained after the roots were freed from the bending force, and by measurement the convex side lengthened about 1^{mm}, and the concave side shortened about 1^{mm}. The shortening was of course all due to forcible compression, and yet after separation of the tissues, the cortex on the concave side, both in water and in 10 per cent. KNO_3 was somewhat longer than the axial cylinder. The cortex on the convex side was much longer than the concave cortex or the axial cylinder. This seems to make it rather improbable that the compression to which the concave side of the root may be subjected when it curves in response to a stimulus is sufficient to make the cortex shorter than the axial cylinder. Consequently when the cortex of the concave side does become shorter than the axial cylinder, as was found to be the case in some of my experiments (table VII), it must be explained on other grounds than passive compression. That there is such a shortening of the cortex on the concave side in its relation to the axial cylinder is shown by experiments performed by Sachs (62) and Ciesielski (5), who found that when the root is split into halves and the half root is placed in a horizontal position with the cut face upward, the half root sometimes remains straight, sometimes curves upward and sometimes curves downward; whereas, if the half root is laid with the cut face turned downward, the curve is invariably downward. It has already been noted in this paper (page 32) that when roots are split after they have begun to curve away from the brand on one side of the tip and the halves have been placed in an upright position, the curving of the concave half root toward the cut face is delayed, though it usually takes place later. The stimulus of burning one side of the root is a strong stimulus but applied for only a short time, and when the reaction from the effects of the stimulus sets in there is no further stimulating effect. When roots are laid in a horizontal position, however, the stimulus is continuous and its effects therefore are cumulative so long as the root tips do not attain a vertical position. For this reason the stimulus of gravitation is

preferable to that of injury for showing the effect of stimuli on the relation of axial cylinder to the cortex on the concave side of the curving root. I have therefore used gravitation as the stimulus in the following experiments. Seedlings of *Cucurbita Pepo* with roots 5–20^{mm} long were placed in a horizontal position in moist air, and when the curve had begun to show or before, the roots were split in the growing region and the upper or convex half of the tip was removed. For control observations roots were left whole or the lower half of the tip was removed. Thirty-four roots with one half of tip removed were placed in a horizontal position in moist air with the cut face upward. In two to four hours ten had curved slightly upward, six had curved slightly downward at tips, the others, eighteen in number, remained straight. In six to eight hours fifteen had curved more or less upward, eight downward, and eleven still remained straight. After twenty-four hours eleven were curved upward, and eighteen were curved downward.

As control for these, thirteen roots were laid in a horizontal position without injury. They all turned downwards within six to eight hours. Also seventeen roots were split and laid horizontal with cut face down. They likewise had all turned downward within six to eight hours, and some of them had formed a curve of 90° within two hours. There was, therefore, a very remarkable difference between the behavior of those roots which had the cut face of the split tip turned down and those which had the cut face turned up. While the former began at once to curve in toward the cut face, and the curve was completed rapidly, the latter nutated up and down for some time, and even at the end of twenty-four hours after splitting it was still undecided in which direction some of them would curve. In the thirty-four roots observed a larger number at first started to curve upward, and a few continued to curve in that direction. Others of this number later reversed the curve and finally turned downward. They sometimes showed a double curve, the split part farthest from tip turning up, but nearer the tip turning down. The same root often nutated up and down several

times before the direction of the curve was finally determined. At the end of twenty-four hours more than half were turned down at the tips, some of these tips being in a vertical position, others only slightly below the horizontal. This behavior indicates beyond doubt that there is a shortening of the cortex in relation to the axial cylinder on the side of the root that becomes concave, for in these roots with the upper half of the tip removed there can be no compression of the cortex on the lower side by the increased growth or extension of the cortex on the upper side, and the normal tension between the cortex and axial cylinder of a half root is such as to cause it always to curve with the cut face concave. It has already been shown that a half root stimulated on the outer side of the tip curves with the cut face concave not only more rapidly than a whole root so stimulated, but also more rapidly than an unstimulated half root (*fig. 1*). We are forced to the conclusion that a stimulus to the root increases the tissue tension between axial cylinder and the cortex on the side that becomes convex, and decreases or reverses the tension between the axial cylinder and the cortex on the side that becomes concave. These changes on the opposite sides of a curving root are independent of each other, and neither side of the root is passive in the curvature, but both are active in producing it. Those theories, therefore, which attempt to account for the curvature by a change on only one side of the root, whether on the convex or concave side, cannot be accepted.

I have made numerous attempts to find a difference in the turgor of cells on the concave and convex sides of the curving root, but was not able to demonstrate such a difference. Solutions of KNO_3 of varying strength were used, and the two sides always plasmolyzed in the same solution and in the same time. In a few cases it was noticed that the cells of stimulated roots plasmolyzed with a weaker solution than straight uninjured ones that had been under precisely the same conditions. The point was not pursued far enough to show whether or not the difference was merely an individual variation.

MEASURING CELLS.

In measuring cells in *Vicia faba* roots it was found that in those which were strongly curved, most of the cells of the cortex on the concave side between the zone of the greatest curvature and the tip had their radial diameter longer than the diameter parallel to the long axis of the root. This is true to about 3^{mm} from the tip of strongly curved roots, but beyond that point the cells elongate rapidly, so that the radial diameter becomes shorter than the one parallel to the long axis of the root. The fact that the cells in the region mentioned have the radial diameter greater than the other is positive proof against Kohl's contraction theory as applied to these roots. Any contraction necessarily takes place partially in this region, and according to Kohl's theory the increased turgor shortens the longer diameter of the cells on a concave side. It is inconceivable, however, that the longer diameter could become the shorter one through increased turgor. Since the cell diameter parallel to the direction in which the cells are supposed to shorten is less than the diameter transverse to that direction after the curve is produced, it is obviously impossible for the shortening of the concave side to be brought about as Kohl supposed. In the discussion of grass nodes Kohl himself writes (**33**, p. 49): "The transverse diameter of the concave cells is greater than the longitudinal diameter." But Kohl evidently did not see that this condition invalidated his theory of curvature.

WATER CONTENT OF CONVEX AND CONCAVE SIDE OF CURVING ROOTS.

In a series of experiments I have determined that there is a greater relative amount of water in the convex half of curving roots than in the concave half, but this is just what should be expected if we take into consideration the enormously large vacuoles on the convex side as compared with those on the concave side. As I do not consider these results of very great importance, I shall not give them in full, but only a summary.

The method was as follows: roots were branded as usual, and after the curve had made considerable progress, the roots

were separated into two lots, one for the control of the other. The average time was about six hours after branding, and the extreme limits were 3.5 and 11.5 hours after branding. In the control experiments the roots were taken from water and the outside carefully wiped with a dry cloth to get rid of the water adhering to them, and just enough of the tip was cut off to take in all the curve. These tips were put into a weighing flask, which was closed air tight. In the other experiments the roots were split into two parts as nearly equal as possible, one half being the concave, the other the convex side of the curve. The two halves were cut off by a cut transverse to the root at the point of cutting, and just enough taken to include the whole curve. The convex halves were put into one flask, the concave halves in another. The flasks had all been previously weighed, now the weight of the roots was ascertained. They were then dried quickly at a temperature of 100° C. until they ceased to lose weight, and were weighed again. The loss in weight, which equals the amount of water, was calculated on the basis of the fresh weight.

A total of 143 roots were split and seventy-three were taken without splitting. The control and the split roots were weighed in fourteen different lots of each. With the exception of one lot they all showed a greater percentage of water in the convex halves than in the concave halves. That one exception was the one in which the time was the shortest, and the excess of water in the concave side was only 0.07 per cent. In the other lots the extreme limits of variation were 0.08 per cent. and 1.9 per cent. in favor of the convex side. The total amount of water varied from 87.42 per cent. to 91.93 per cent. in the convex side and from 87.49 per cent. to 90.86 per cent. in the concave side. In the whole tips the variation was from 85.96 per cent. to 91.15 per cent. One third of the lots of the latter showed a greater amount of water than the corresponding split roots. One third were between the convex and concave sides of the corresponding split ones, and one third fell below the concave side in the corresponding lots.

Another series of control experiments was used in which straight roots were split into halves, and the water content of the separate halves ascertained as before. The stimulated roots were all branded on the side of the tip facing the hilum of the seed, so that side was always the convex side of the curve. The straight unstimulated roots were always split in the corresponding plane and a record kept as to which was the side next to the hilum. So the two series were exactly comparable. The lots were nearly all treated at the same time and under exactly the same conditions as the curved ones. A total of fifty-nine straight roots were split and weighed in six different lots. The variation on the side next the hilum, corresponding to the convex side of the curved roots, was from 87.72 per cent. to 92.51 per cent., and on the opposite side from 87.63 per cent. to 92.49 per cent. In three lots the excess was on the hilum side and in three lots on the opposite side.

Nothing has been proved as to the absolute increase or decrease of the water content in stimulated roots, but it is shown beyond a reasonable doubt that there is a relative increase of water in the convex side of curving roots. This does not prove, however, that the greater amount of water on the convex side increases the size of the cells. It may simply mean that the increased size of the cells enables them to hold more water with the same turgor pressure. Indeed, the increased amount of water must necessarily reduce the concentration of the cell sap and therefore the osmotic pressure, unless there is at the same time an increase in the production of osmotic substances in those cells. I know of no evidence for such an increased production of osmotic substances, and Kraus has shown that there is a relative and absolute decrease in osmotic substances on the convex side during the later stages of the curve. My results agree with his as to the increase of water on the convex side.

SUMMARY OF EXPERIMENTS.

The experiments submitted justify the following conclusions:

1. The transmission of the stimulus from the sensitive tip to that part of the root which curves takes place in the cortex. It may take place in the cortex of either the side that becomes concave or that which becomes convex, and is not restricted to the side on which the root tip is wounded.

While it is not absolutely demonstrated that transmission cannot take place in the axial cylinder the evidence is strongly against such an assumption.

2. The stimulus may be transmitted in the transverse or tangential direction as well as in the longitudinal direction.[4]

3. The mechanism of root curvature, as in curvature of stems, is closely connected with the tissue tensions existing in the organ previously to stimulation.

4. The ordinary tissue tension of roots is the reverse of that in stems. That is, the outer cortical parenchyma is under positive tension, the central cylinder under negative tension. Three lines of evidence show this to be true ; first, the rupturing of the central tissue in rapidly growing roots ; second, the curving in of split roots with the cut face concave ; third, the difference in length of the cortex and axial cylinder when separated from each other. It is not uncommon in *Vicia faba* roots for this difference to be as great as 10 per cent. of the length of the separated tissues, when the separation is for 1^{cm} back from the tip.

5. Stimulation causes an increase of the tension between the axial cylinder and the cortex on the side which becomes convex, and decreases or reverses the tension between the axial cylinder and the cortex on the side that becomes concave. The shortening of the concave side may be merely relative or there may be an absolute shortening as has been shown by Kohl and myself. That the shortening is not due merely to compression by the more rapid extension of the cortex on the convex side is proven by the behavior of split roots that are laid in horizontal position

[4] A recent article by Ewart (20) shows that in the climbing hooks of various tropical plants the stimulus is transmitted in a transverse or tangential direction from the concave side, which alone is sensitive to contact, pressure, and injury, to the cambium which is incited to increased growth.

with the cut face upward. The up and down nutation exhibited
by roots in that condition can only be due to the varying tension
between cortex and axial cylinder in the half root that becomes
concave; and the fact that more than half of the roots experi-
mented upon in that way finally curved downward proves that
the tension may be often reversed in the concave half of the
root. This conclusion is also indicated by the relative length
of the separated tissues of curved roots, though in these cases
compression of the concave cortex is not eliminated. Experi-
ments similar to those just mentioned, but with different details,
prove the increased tension on the convex side.

6. Not only is the tension between the axial cylinder and the
cortex on the side that becomes concave changed by the stimu-
lus, but the different layers of the cortex itself change in their
tensile relations to one another. In curving roots the outer lay-
ers of the cortex on the concave side are under negative tension
in relation to those layers lying more central. This is shown by
the fact that when the tissues of curving roots are separated the
concave cortex curves more than the whole root has done, often
curving with a sudden jerk as soon as separated, and forming a
curve with a very short radius. That this is not due to the nor-
mal tension of the epidermis and root cap is shown by compari-
son with the convex cortex and with the isolated cortex of
unstimulated roots. It is not impossible that forcible compres-
sion of the outer layers of the concave side may sometimes play
a part here. Such compression necessarily takes place in the
outer layers of this side notwithstanding its shortening, unless
the outer layers are shortened more than the inner ones as a
direct result of the stimulus. If the greater shortening of the
outer layers was merely the result of compression, we should
expect them to lengthen when freed from that compression, and
the isolated cortex would then straighten. Since the isolated
cortex curves more strongly than before isolation, it seems prob-
able that the change produced directly by the stimulus in the
cells of the concave side is greater in the outer layers of that
side than in the inner layers.

The root reacts to the stimulus as a whole, and is not affected merely on one side. The changes in the cells of the two opposite sides, which become respectively concave and convex, are opposite in their effects, and these changes are coordinated so as to bring about the curvature with a fairly economical expenditure of energy, so far as this is indicated by the tissue tensions. It is remarkable that a stimulus may be transmitted in one side of the cortex past a deep gash in the opposite side, and yet above the gash produce opposite effects on the opposite sides of the root. The mechanism of the curvature is a more complicated problem than some writers on the subject have imagined.

7. In the traumatropic curvature of *Vicia faba* roots, the zone of maximum curvature does not coincide with the zone of maximum growth, but is nearer the tip. In four to eight hours after the beginning of the curve, it is mostly in the first half-centimeter from the tip, while the greater growth during the same period is in the second half-centimeter from the tip. Within twenty-four hours, however, the zone of maximum growth meets and may even pass the zone of maximum curvature.

8. The proportions of cells in the curving part of Vicia roots are such that Kohl's theory of the curvature cannot possibly be true for them.

9. The cells of the convex half of curved roots contain a larger quantity of water than those of the concave half.

Theoretical considerations.

After examining carefully the experimental evidence we are forced to the conclusion that no theory yet advanced is adequate for the explanation of all curvatures due to stimulation. Sachs' earlier view that there is merely a difference in the rate of growth on the opposite sides of the curving organ does not explain satisfactorily the contraction often observed on the concave side; and even if it did explain this contraction it would not be a complete explanation of the curvature, because we do not yet know what growth really is; nor do we know the immediate source of the energy of growth. The evidence is against de Vries' view

that there is an increased turgor on the convex side of the curv-
ing organ. Wiesner's view that when the root tip is injured on
one side the cell membranes on that side above the wound are
made more extensible, does not account for the changes on the
opposite side which are indicated by'my experiments. Wiesner
makes a distinction between geotropic and traumatropic curva-
tures. In the case of the former he supposes an increase of
ductility of the cell membranes on the side becoming convex,
and also an increase in the elasticity of the cell membranes on
the side which becomes concave. Even though we admit that
a sufficient increase in the elasticity of the membranes on the
concave side could shorten the cells by forcing water out through
the protoplasm, we may well doubt whether that is the method
by which the cells are shortened, until further evidence has been
presented in favor of that view. We must believe that the
elasticity of the membranes is brought about only by the activity
of the protoplasm ; and it does not seem to be an economical
expenditure of energy for the protoplasm to increase the elasti-
city of the walls until their pressure forces water out through
the protoplasm, when by its activity it can change its permea-
bility to water and allow the cells to shorten without increasing
the elasticity of the cell walls. It has already been shown (p. 44)
that the concave side shortens in relation to the axial cylinder
when compression by the cortex of the convex side is out of the
question.

Nöll supposed he had proved the greater extensibility of the
membranes on the convex side of curving stems by his bending
experiments. With the same pull the stems bent more toward
the concave than toward the convex side. It has been shown
(p. 26) that this is the necessary result of the tensions in stimu-
lated stems ; therefore it is evidence only of those tensions, and
not at all in favor of any particular method by which those
changes from the normal tension are brought about. Noll
showed by other methods that the size, and the optical and
staining properties of membranes on the convex side were differ-
ent from those of unstimulated stems ; and it may be that the

membranes on that side are really more extensible than those of normal stems. My own experiments show that the convex half of the stimulated roots which are split when the curve begins, curve much more rapidly that the similar half of unstimulated roots; and to that extent my experiments may be said to support the view that the convex side of stimulated organs is more extensible than similar cells of normal organs. But that this is the only factor, or even the main one, in the curvature of stimulated organs is disproved by the experiments of Sachs and Kohl for stems, and my own experiments on roots, which show that in both stems and roots changes also take place in the concave side of an opposite kind from those in the convex side. Enough has been said to show that MacDougal's conclusions as to the mechanism of root curvature cannot be accepted as adequate.

Since the theories of Wortmann, Kohl, and Loeb all regard the concave side as alone active in the formation of the curvature, they are inadequate at the best. They take no account of the decreased tension in the convex side of curving stems, and the increased tension in the convex side of curving roots. Wortmann's theory also fails to account for the contraction of the concave side. Moreover, objections have been made to it by Noll, Kohl, and others which remain unanswered, and probably are unanswerable.

Aside from the inadequacy of Kohl's theory as a complete explanation of the curvature, it is not even proven as the cause of contraction of the concave side. While theoretically possible, perhaps, it requires that the cells in the region of curvature have their longer diameter parallel to the longitudinal axis of the curving organ. Kohl's own work shows that this condition does not exist in grass nodes, and my observations show that it does not exist in the tip half of the curved zone of *Vicia faba* roots. Moreover, Kohl's theory would seem to require that at the beginning of plasmolysis the cells of the concave side should lengthen, and the curve be somewhat straightened ; but Kohl and Noll both found an increase of the curvature at the beginning of plasmolysis, when the curve was not too old.

Loeb seeks to explain the contraction of the concave side in curving plant organs by the same process as the contraction of animal muscle. He states that in an active muscle there is an increase of osmotic substances, and that a weighted contracting muscle takes up more water than a resting one. He points to the observations of Kraus as proof that osmotic substances are increased in the cells of the concave side of curving plant organs. He offers no proof or evidence, however, that these cells take up more water than the cells of the convex side. Indeed all the evidence is against it. My weighing experiments with the concave and convex halves of curving roots prove beyond doubt that the convex side contains more water than the concave side. Hence the contraction in plant cells cannot be the same as in animal cells. Pulvini also show a loss of water in the cells of the contracting side. Loeb does not consider sufficiently the contracting power of the elastic membranes of turgid plant cells, which may contract with a decrease of osmotic pressure.

When we consider the varied mechanical conditions which are found in such plant organs as fungus hyphæ, grass nodes, dicotyledonous stems, and roots, we should hardly expect, even *a priori*, that a single explanation of curvature would apply to all plant organs. How much less should we expect that a single explanation would apply not only to all plant curvatures but also to contractions of animal muscles, and to free movements of both plants and animals, as Loeb would have us believe. The experimental evidence is against this view.

Pfeffer has shown that in grass nodes the curve is brought about by an active growth of the collenchyma bundles of the convex side. Even here a certain amount of potential energy, which exists previously to stimulation in the form of the positive tension of the parenchyma, becomes available for growth of the collenchyma. In their growth the walls of these collenchyma cells undergo those changes which Noll says indicate plastic stretching and greater ductility of the membranes. That the walls are more ductile may be admitted and the ductility still be

regarded as a phenomenon of growth. Similar changes in the membrane have been shown by Strasburger to accompany growth in the formation of new branches of Cladophora. Whether the shortening that has been frequently observed on the concave side of curving grass nodes is due to compression merely or to active shortening has not been demonstrated.

The climbing hooks of various tropical plants investigated by Ewart in Java (20) are examples of organs which respond to stimuli by increased cambial growth and cell division. Here also the mechanical relations of the tissues are such that neither mere changes of turgor on opposite sides nor any plastic or elastic stretching could produce the response to stimuli which these organs show. The curve of the hook may be increased by a greater growth on the convex side; or the hook may be made to clasp a support merely by an increase in the transverse diameter which diminishes the diameter of the circle already formed by the normally curved hook. In either case the response takes the form of growth.

Noll has reported experiments with Hippuris stems which are perhaps of more importance than he supposed (50, p. 51). The stems were laid in a horizontal position in air not saturated with moisture and they were not in contact with liquid water. Nevertheless they curved upward in a U-shape; and the lower convex side was smooth, shiny and turgid, while the upper concave side became wrinkled and limp. Since the stem could get no water from the outside, any increase in the amount of water in the cells on the lower side must have come from the cells on the upper side. The water could not have been forced out of the cells on the upper side by mechanical pressure from the lower side, because that pressure could have been exerted only after the lower side had obtained more water. Either the cells on the lower side withdrew water from the cells on the upper side by a greater osmotic power, in which case the water would not pass into the intercellular spaces; or the cells on the upper side, affected directly by the stimulus, allowed the water to pass into the intercellular spaces, and the water was then taken up by the

cells on the lower side. I see no other alternative. Greater extensibility of the membranes on the lower side could not enlarge the cells unless they took up more water. The evidence is against the greater osmotic pressure on the lower side; and the conclusion seems inevitable that the cells on the upper side, from the immediate effect of the stimulus, allowed water to escape into the intercellular spaces. This could be brought about either by increased elasticity of the walls or increased permeability of protoplasm to water. From what we know of effect of stimuli on other plant organs, the latter view seems more probable, though it is possible that both the elasticity of the walls and the permeability of the protoplasm are increased by the stimulus. If the stimulus can cause the cells on the upper side of a horizontal Hippuris stem to give out water into the intercellular spaces as a direct effect, we are justified in thinking that the shortening of the concave side in other stems and in roots also can be brought about in the same way. Noll has observed that when curving stems have been gashed on one side, water is gradually forced out of the gash, and shows in the form of drops. The water must have come from the intercellular spaces into which it had escaped from the cells on the concave side.

MacDougal asserts (**39,** p. 309) that there are no intercellular spaces in the motor zone of roots into which water could pass from the cells. He is certainly mistaken as regards *Vicia faba* roots in which well developed intercellular spaces are found in the cortex very near to the initial zone. In sections from fresh roots their presence is easily demonstrated by the air contained in them. MacDougal himself, however, says in another place (**39,** p. 309) of the roots of *Zea mais*: "Intercellular spaces (of the convex side) are larger and more abundant than in the concave side." Evidently there are intercellular spaces in roots of Zea also. This makes the condition favorable for water to escape from the cell if the protoplasm becomes more permeable. That the stimulus produces this condition in roots has not been proved; but it seems to me to be the most reasonable explanation of the phenomena exhibited in the concave side of curving

roots. The loss of water due to greater permeability of the protoplasm accounts for the decrease or the reversal of the tension between the cortex and axial cylinder on the concave side; and it is especially satisfactory in explaining the actual shortening of the concave side which has been so often observed by different men in grass nodes, dicotyledonous stems, and roots. In answer to the objection that mechanical compression may also shorten the concave side, I have already shown (p. 44) that there is at least a relative shortening of the concave side under conditions where compression cannot possibly be exerted by the convex cortex in the case of roots; and Noll's Hippuris stems show the same thing for dicotyledonous stems. The objection that greater elasticity of the cell membranes may cause the shortening is answered on p. 51; but this elasticity is not excluded absolutely as one of the factors in the curvature.

Noll has pointed out that in wilting plants the cell sap may become more concentrated and its osmotic equivalent greater while turgor falls; hence the greater permeability of the protoplasm in the cells of the concave side is not contradictory to those observations of Kraus and Kohl which show an increased amount of osmotic substances on the concave side. Indeed it may be that the very activity by which the protoplasm becomes more permeable results in an increased production of osmotic substances, as Vines has pointed out.

The loss of water through greater permeability of the protoplasm on the concave side is not disproved by the fact that the concave side often lengthens more or less during the curvature. Turgor might sink quite appreciably from the loss of water and the cells still be capable of growth in length; and in those cases which lengthen, this growth more than counteracts the shortening effect. If the cells did not grow in length the walls could still grow in thickness, and the thickened walls observed by Wortmann are thus accounted for.

The time required for root curvatures cannot be regarded as evidence against the increased permeability of protoplasm in them, for MacDougal has found that tendrils coil in response to

contact by allowing water to escape from cells on the concave side, and the reaction may take as long as 1⅔ hours (**38,** p. 376). Roots often curve 90° within two hours.

The shortening of the cells on the concave side by allowing water to escape is also in harmony with the results of Noll's bending experiments, since, as I have previously shown, those results are merely the expression of the tissue tensions in stimulated organs, and indicate nothing as to the particular method by which those tensions are produced.

It has already been mentioned that Noll and Kohl both found, in the early stages of the curve, an increase of the curve on first putting the organ into a plasmolyzing solution, and this plus curve was followed only later by the straightening of the organ. Each of these men claimed that the plus curve was in harmony with his theory of the curvature; but the criticism of Noll's argument compelled him to admit that the problem was more complex than he had supposed and that he had not explained the plus curve. I am totally unable to see the logic in Kohl's argument, or to see how his theory explains the plus curve at the beginning of plasmolysis. On the other hand it seems to me easily explainable on the theory that the protoplasm in the cells of the concave side becomes more permeable to water. If we suppose that the protoplasm becomes more permeable by an increase in the size of its molecular interstices, then a given amount of energy, whether exerted by the elasticity of the cell walls or by a plasmolyzing solution outside of the cell, will withdraw a given amount of water from the cell *in a shorter time.* Hence when a curving root or stem is placed in a plasmolyzing solution a plus curve necessarily follows at first, if the protoplasm of the concave cells is more permeable; but while the convex side plasmolyzes more slowly, since its protoplasm is less permeable, the cells on that side finally shorten more than the cells on the concave side, and the end result is a straightening of the whole organ.

Some observations of Kohl seem to contradict the view that the cells on the concave side plasmolyzed more rapidly than on

the convex side. Kohl says he found constantly that the pro-
toplasm in the cells of the convex side pulled away from the
cell wall sooner than in the cells of the concave side. If there
is a real contradiction here it is not so much between Kohl's
observations and the greater permeability of the protoplasm in
the concave cells as between the two series of observations
made by Kohl himself, one showing tl at plasmolysis gives a
plus curve at first, and the other that the convex cells plasmo-
lyze sooner. There appears to me a possibility however, that
makes the contradiction only apparent and not real. MacDou-
gal found in tendrils which were plasmolyzed, then fixed and cut
into thin sections, that the protoplasm of the cells on the convex
side was pulled completely away from the wall, while in the
outer rows on the concave side it was barely separated from the
wall. Nevertheless the tendril, when plasmolyzed, had increased
its curvature and MacDougal believes he has shown that the
protoplasm becomes more permeable in the cells of the concave
side. The explanation seems to me to be that the protoplasm
becomes more permeable not only for water, but also for the
plasmolyzing solution. Hence the protoplasm in the cells of
the concave side allows the KNO_3 to pass inward to a greater
or less degree, while that in the cells of the convex side resists
penetration by the plasmolyzing solution, and on the convex
side the protoplasm is forced away from the walls sooner and
more completely than on the concave side. Some observations
of my own seem to show that the protoplasm in the parenchyma
of *Vicia faba* roots can become permeable to KNO_3. In
numerous sections the protoplasm in the cortical parenchyma
was not contracted from the walls even in a 10 per cent. solu-
tion, though the cells had completely lost their turgidity I was
not able to see any difference in the pulling away from the wall
of the protoplasm in the cases which showed that phenomenon,
even when Kohl's method was used. My observations on that
point were not extensive, however. Different observers have
reported quite different results as to the plasmolysis of cells
of the convex and concave sides, and the point probably needs

further investigation.   On the whole, the view that the proto-
plasm in the cells of the concave side becomes more permeable
seems to explain more phenomena than any other view yet
advanced ; and while it is not absolutely demonstrated, I believe
it to be the condition which lies at the basis of those changes
which, as my experiments show, take place in that half of a
stimulated root which becomes concave.

As for the changes which take place in the half that becomes
convex, there is certainly an increased growth on that side ; and
Noll has shown that there is in some cases a change in the qual-
ity of the membrane.   It is not proved, however, that this
change in the membrane is a condition preceding growth, as
Noll believed, since it may be merely the method of growth.
This point can be decided only when our knowledge of the
mechanics of growth is more complete.

In the light of the foregoing experiments and arguments the
mechanism of the curvature of roots is as follows : The stimulus
is transmitted from the sensitive root tip to the curving parts, in
the cortical parenchyma.   The effect of the stimulus is to
increase the normal tension between cortical parenchyma and
axial cylinder on the side that becomes convex, and to decrease
or reverse the normal tension between the cortical parenchyma
and the axial cylinder on the side that becomes concave.   The
change in tension also extends to the different layers of the cor-
tical parenchyma on the concave side, the outer layers becoming
negative with respect to the inner ones.   So much has been dem-
onstrated.   The evidence is in favor of the view that the ten-
sions on the concave side are changed by the protoplasm becom-
ing more permeable to water, some of which passes out into the
intercellular spaces, possibly to be taken up by the convex cells,
which later contain more water than the concave cells.   The
shortening of the concave side may be masked sometimes by a
certain amount of growth.

The same explanation will apply to curvatures of dicotyle-
donous stems if allowance is made for the different normal ten-
sions found in them.

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